SHORT COMMUNICATION

Response of plant roots to elevated atmospheric carbon dioxide

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ABSTRACT

Plant root response to atmospheric CO_2 enrichment can be great. Results from this controlled environment investigation demonstrate substantial effects on root system architecture, micromorphology and physiology. The most pronounced effects were an increase in root length (110%) and root dry weight (143%). Root diameter, stele diameter, cortex width, root/shoot and root weight ratios all increased; root numbers did not increase. The long-term implications for belowground processes could be enormous.

Key-words: Glycine max; soybean; CO_2 enrichment; root architecture; root micromorphology.

Predicted shifts in climate (Bolin *et al.* 1986) and expected increases in atmospheric CO_2 concentration (Keeling *et al.* 1989) are critical parts of the changing global environment. Whether or not climatic shifts occur, rises in CO_2 concentration will directly impact vegetation (Rogers, Thomas & Bingham 1983; Wittwer 1985). Not only is CO_2 a major greenhouse gas, i.e. radiatively active, but it is essential to plant life and also stimulates growth (Kramer 1981; Dahlman, Strain & Rogers 1985; Warrick 1988). An overlooked and under-studied aspect of plant response to rising CO_2 concentration is that of belowground processes. The vital role of roots as an interface between the lithosphere and biosphere is of pivotal significance in moving toward a fuller understanding of plant reaction to elevated CO_2 concentration. Data dealing with effects of CO_2 concentration on belowground plant responses exist but are few and far between (Tognoni, Halevy & Wittwer 1967; Chaudhuri, Kirkham & Kanemasu 1990; Del Castillo *et al.* 1989). Research in this area is warranted and a recommendation to remedy this paucity of information has been made (Strain & Cure 1985). The objective of this work is to explore the spatial and functional aspects of plant rooting under elevated CO_2 concentration and to help provide heretofore missing data for simulation models that address the effects of CO_2 concentration on

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belowground plant processes. The response of root systems of plants grown under elevated CO_2 concentration is of signficance to: the plant's capacity to mine soil profiles for mineral nutrients (Luxmoore *et al.* 1986) and water, which are critical during stress; carbon flux to soil; the soil as a sink in the global carbon budget; and the potential modification of soil characteristics.

Soybeans [*Glycine max* (L.) Merr. 'Lee' nonnodulating] were grown in controlled environments of the Duke University Phytotron (Kramer, Hellmers & Downs 1970) at two concentrations of CO_2, 350 and 700 μmol mol^{-1}, for 18 d. The growth medium was perlite (16 replicates of 17 dm^3 pots for each CO_2 treatment) watered with a modified Hoagland's solution (Downs & Thomas 1983). A growing regime of 9-h days was used at a quantum flux density of 1000 μmol m^{-2} s^{-1} (400–700 nm) with day/night temperatures of 26/22°C and relative humidity, 55–65% during the day and 75–85% at night.

At harvest, four of the replicates were processed for determination of total plant N (Bremner & Mulvaney 1982). Nitrogen uptake efficiency was determined by dividing total N by the surface area of the root system. The remaining 12 replicates were assessed for shoot and root geometry. Detailed measurements of the size and location of root component parts were made. Mass of the plant component parts and root volume, based on water displacement, were measured. Microscopic comparisons of leaf and root anatomy were made by thin sectioning plastic-embedded samples.

There was a notable difference in the overall appearance of plant root systems between the two CO_2 concentrations (Fig. 1). The root system of the 700 μmol mol^{-1} specimen would appear to have a greater sorption capacity based on its size. Table 1 contains a summary of plant variables; those associated with roots stand out compared to shoot values. High CO_2 increased leaf area and thickness. All variables except number of stem nodes and number of lateral roots increased, and all increases were statistically significant (Schlotzhauer & Littell 1987). Roots exhibited a far greater enhancement of growth than did shoots (e.g. leaf and stem dry weights increased 90 and 75%, respectively, whereas root dry weight increased 143%). Total root length more than doubled, but the number of first-order laterals was

Figure 1. Photographs of 18-d-old soybean plants grown at (a) 350 µmol mol^{-1} and (b) 700 µmol mol^{-1} CO_2. Photographs show the median plant, based on root length, for each treatment.

Plant measurements	CO_2 treatment		Per cent increase	Significance
	350 µmol mol^{-1}	700 µmol mol^{-1}		
Geometry				
Leaf area (cm^2)	163·3 ± 5·2	255·4 ± 5·8	56	**
Leaf thickness (µm)	117·0 ± 4·3	131·0 ± 3·6	12	*
Stem height (cm)	21·5 ± 0·3	24·7 ± 0·8	15	**
Stem diameter (mm)	2·95 ± 0·08	3·49 ± 0·07	18	**
No. of stem nodes	4·0	4·0	0	NS
No. of lateral roots	161·5 ± 6·0	162·5 ± 5·3	0	NS
Root length (m)	12·5 ± 0·5	26·3 ± 0·8	110	**
Root volume (ml)	4·1 ± 0·3	7·4 ± 0·5	80	**
Dry weight (g)				
Leaf	0·41 ± 0·01	0·78 ± 0·03	90	**
Stem	0·20 ± 0·01	0·35 ± 0·01	75	**
Root	0·14 ± 0·01	0·34 ± 0·01	143	**
Total plant	0·76 ± 0·02	1·47 ± 0·03	93	**
Ratios				
Root/shoot ratio	0·23 ± 0·01	0·30 ± 0·02	30	**
Root weight ratio	0·18 ± 0·01	0·23 ± 0·01	28	**
Root microscopy				
Root diameter (µm)	776 ± 29	982 ± 57	27	**
Stele diameter (µm)	202 ± 7	249 ± 17	23	*
Cortex diameter (µm)	287 ± 12	366 ± 21	28	**

Table 1. Effect of CO_2 on growth components of soybean [mean ± standard error, per cent increase, and significance (ANOVA); $n = 12$]. Root microscopy was performed on plastic embedded sections from the root hair zone
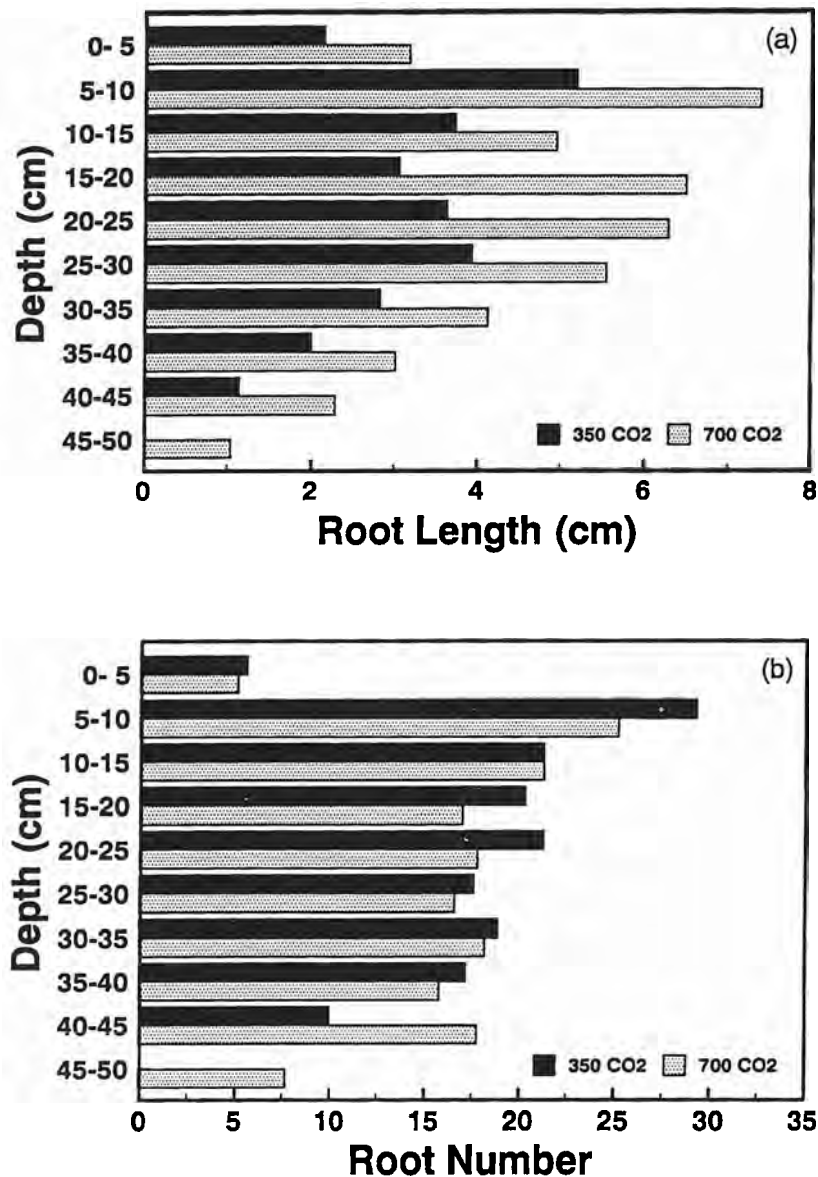
*$P = 0·05$.
**$P = 0·01$.
NS: not significant.

Figure 2. (a) Length of first-order lateral roots with depth (n = 12). (b) Number of roots for the same 12 soybean plants with depth.

unaffected. Elevated CO$_2$ concentration significantly increased the volume of the root system (taproot plus all laterals). Root/shoot ratio (root dry wt/shoot dry wt) and root weight ratio (root dry wt/total dry wt) were boosted. Root diameter was 27% greater in the root hair zone. Light microscopy revealed a 23% increase in stele diameter and a 28% increase in cortex width.

Figure 2 shows the mean length and number of first-order lateral roots at 5-cm increments for both the 350 and 700 μmol mol^{-1} grown plants. Consistent and significant (0·01 level) increases in first-order lateral length were observed and root penetration under the elevated CO$_2$ concentration was deeper (no 350 μmol mol^{-1} CO$_2$ roots below 45 cm; Fig. 2a). Figure 2b shows

the pattern of first-order laterals with depth; treatment differences are not significant for number.

These findings demonstrate that CO$_2$ enrichment enhances root growth much more than that of shoots, increasing root diameter, length, volume, and weight. Dry weight ratios (taproot/lateral roots) suggested a differential CO$_2$-enhancement of taproots and laterals; average ratios were 0·91 at 350 μmol mol^{-1} and 0·38 at 700 μmol mol^{-1}. Root length, especially of lateral roots, was the single most pronounced root morphological effect of increased CO$_2$ concentration as was suggested by Tognoni *et al.* (1967). Increased root length implies the probability of deeper soil penetration and access to deeper reservoirs of water, as well as the possibility of

more thorough mining of the soil profile for nutrients. Total N uptake per plant increased (35·5 and 63·0 mg N for 350 and 700 μmol mol^{-1}, respectively); however, calculated average N uptake efficiency per unit root surface area did not appear to be affected by CO_2 (0·140 and 0·127 mg N cm^{-2} root surface for 350 and 700 μmol mol^{-1}).

Carbon dioxide often suppresses plant water use (Kimball & Idso 1983; Rogers et al. 1984), boosting water use efficiency (i.e. carbon fixed/water transpired). Since higher water use efficiency means relatively less water flow within the plant body and consequently in the soil matrix, the greater proliferation of roots grown under elevated atmospheric CO_2 concentration may be a strategy which permits adequate nutrient acquisition in the absence of normal water absorption rates. The deeper roots could penetrate, the more resilient to droughts natural plant communities and agronomic crops would become. This deeper rooting would be an advantage if climates became drier. Belowground plant competition could be altered. The increased early root growth observed here implies that plant roots could act as sentinels of atmospheric CO_2 accumulation. The CO_2-enhanced root growth found in this study suggests: the delivery of more carbon to soil profiles; potential alteration of rhizosphere microbiology (populations and dynamics); and possible physicochemical changes in soil brought about by increased root activity, including rhizodeposition. This work is currently being extended to include interactions with edaphic stresses. Also, field research efforts using free-air CO_2 enrichment have been initiated.

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